

Gastrointestinal Digenetic Trematodes of Olive Ridley's Turtle (*Lepidochelys olivacea*) from Oaxaca, México. Taxonomy and Infracommunity Structure

GERARDO PÉREZ-PONCE DE LEÓN,¹ LUIS GARCÍA-PRIETO AND
VIRGINIA LEÓN-RÉGAGNON

Instituto de Biología, Universidad Nacional Autónoma de México, México D.F.,
Apartado Postal 70-153, C.P. 04510, México

ABSTRACT: Thirty-two Olive Ridley's turtles (*Lepidochelys olivacea* Eschscholtz) were collected from the coast of Oaxaca, México, and their digestive tracts were examined for helminths. Eight digenetic trematode species were found in the digestive tracts of 24 of 32 turtles: *Adenogaster serialis*, *Himasomum lobatus*, *Pyelosomum renicapite* (Pronocephalidae), *Pachypsolus irroratus* (Pachypsolidae), *Enodiotrema megachondrus* (Plagiorchiidae), *Orchidasma amphiorchis* (Telorchhiidae), *Proisorchis psenopsis* (Hemiuridae), and *Calycodes anthos* (Calycodidae). Oaxaca represents a new locality for all digenetic species and *L. olivacea* represents a new host record for all except *O. amphiorchis*. *Adenogaster serialis* was the species with the highest prevalence of infection (53.1%), while *E. megachondrus* showed the highest abundance (28.2 digenetics/analyzed host). Digenetic community structure at the infracommunity level is depauperate and isolationist according to the values of species richness, numbers of worms, and diversity. Vigility, and the possibility of a mixture of populations arriving at the nesting site, as well as broad feeding preferences, are suggested as the main factors that determine the digenetic community structure in *L. olivacea*.

KEY WORDS: *Lepidochelys olivacea*, Digenetic trematodes, *Adenogaster serialis*, *Himasomum lobatus*, *Pyelosomum renicapite*, *Pachypsolus irroratus*, *Enodiotrema megachondrus*, *Orchidasma amphiorchis*, *Proisorchis psenopsis*, *Calycodes anthos*, infracommunity structure, México.

The Olive Ridley's turtle, *Lepidochelys olivacea* (Eschscholtz, 1829), is one of 7 extant species of marine turtles. All except the loggerhead, *Caretta caretta* (Linnaeus, 1756), are considered endangered (Waldichuk, 1987). The Mexican government has been concerned about the sea turtle stocks of both its Pacific and Atlantic coasts as 6 of the 7 species of sea turtles nest on Mexican beaches (Anonymous, 1988). The coast of Oaxaca State, México, is one of the main nesting areas for *L. olivacea*, but in the last several years nesting populations have decreased. The decrease is mainly because of commercial capture and illegal egg collecting. Development of resort areas near the nesting sites has also caused serious problems for the preservation of this species (Peñaflores and Nataren, 1988). In an attempt to solve these problems, the population biology and nesting behavior of this turtle has been studied intensively (Márquez et al., 1976; Casas, 1978; Frazier, 1983; Enciso and Barajas, 1993). On 31 May 1991, 13 months after our collections, the government initiated a prohibition on the capture of all sea turtles. These regulations also extend to all egg collecting.

Helminth parasites of marine turtles have been examined from a number of hosts and geographic localities (Ernst and Ernst, 1977; Blair and Limpus, 1982; Dyer et al., 1991). Most of the studies in México have investigated the parasites of *Chelonia mydas* (Linnaeus, 1758) (Caballero and Zerecero, 1950; Caballero-Rodríguez, 1960; Caballero 1962). Compared to other marine turtles, relatively little information is available on the parasites of Olive Ridley's. The only previous study on *L. olivacea* from México was by Parra (1983), who reported the occurrence of the digenetic *Plesiochorus cymbriformis* (Rudolphi, 1819) Looss, 1901 and *Pyelosomum cochlear* Looss, 1899. The objective of the present study was to identify and report the gastrointestinal digenetic trematodes of *L. olivacea* and to use patterns of infection to describe the digenetic infracommunity structure.

Materials and Methods

Turtles were collected in Mazunte, 5 km N of Puerto Angel, Oaxaca State, México in March 1990. The turtles were captured by commercial fishermen, taken to Mazunte beach, and killed by shooting. The digestive tracts were the only organs we could acquire from fishermen, because the rest of the body was sold.

The gastrointestinal tracts (esophagus, stomach, and intestine) from 32 Olive Ridley's turtles were refig-

¹ e-mail address: ppdleon@servidor.unam.mx.

Table 1. Digeneans of Olive Ridley's turtles (*L. olivacea*) from Oaxaca, México.

Digenean	Habitat*	CHIBUNAM	USNPC
Pronocephalidae:			
<i>Adenogaster serialis</i> Looss, 1901	I	250-3	84868
<i>Himasomum lobatus</i> (Looss, 1901) Pérez and Brooks, 1995	I	250-11	84872
<i>Pyelosomum renicapite</i> Poche, 1926	I	250-12	84873
Pachypsolidae:			
<i>Pachypsolus irroratus</i> (Rudolphi, 1819) Looss, 1902	I, S	253-12	84874
Plagiorchhiidae:			
<i>Enodiotrema megachondrus</i> (Looss, 1889) Looss, 1901	I	250-10	84871
Telorchhiidae:			
<i>Orchidasma amphiorchis</i> (Braun, 1899) Braun, 1901	I	253-14	84871
Hemiuridae:			
<i>Prosorchiopsis</i> Yamaguti, 1934	S	253-11	—
Calycodidae:			
<i>Calycodes anthos</i> (Braun, 1899) Looss, 1901	I	253-13	84869

* I = intestine; S = stomach.

erated until examination. Digeneans were the only helminth group found. The worms were counted and their site of infection was recorded. They were then collected in petri dishes with 7.5% saline solution and killed with hot water. Most specimens were fixed with Bouin's fixative with light cover glass pressure for 18 hr and then stored in 70% ethanol. Remaining specimens were fixed and stored in 70% ethanol. Specimens were stained with Harris' haematoxylin, Mayer's paracarmine, and Gomori's trichromic and mounted in Canada balsam. Representative specimens were deposited in the Colección Helmintológica del Instituto de Biología UNAM, México (CHIBUNAM) and in the U.S. National Parasite Collection, Beltsville (USNPC) (Table 1).

Prevalence and abundance of each digenean species follow definitions established by Margolis et al. (1982). For description of infracommunity structure, we used the number of helminth species per turtle (richness) and the number of worms per turtle, including uninfected hosts. Brillouin's index, appropriate for fully censused communities (Pielou, 1975), provided a measure of infracommunity diversity. Similarity at the infracommunity level was tested using Sorensen's coefficient (qualitative) and percent similarity (quantitative).

Results and Discussion

Eight digenean species were recovered from 24 of 32 turtles and were identified as belonging to 6 different families, Pronocephalidae, Pachypsolidae, Plagiorchhiidae, Telorchhiidae, Hemiuridae, and Calycodidae (Table 1). No other helminth group was collected. All species found represent new locality records and, except *O. amphiorchis*, new host records.

Taxonomic information

Adenogaster serialis Looss, 1901

One hundred sixty-eight digeneans were identified as *Adenogaster serialis* Looss, 1901. This

is the only valid species included within the genus, because *A. indica* Rao, 1975, reported from *Chelonia mydas* in India, was transferred to *Raogaster* by Groschafft and Tenora (1981).

Adenogaster serialis has a worldwide distribution. It has been reported from *Thalassochelys corticata* (= *Caretta caretta*) in Egypt (Looss, 1901), *Eretmochelys imbricata* (Linnaeus, 1766) in Cuba (Pérez-Vigueras, 1955), and *Chelonia mydas* in Panamá (Caballero et al., 1955) and México, from the states of Guerrero (Caballero-Rodríguez, 1960) and Colima (Parra, 1983).

Himasomum lobatus (Looss, 1901)

Pérez-Ponce de León and Brooks, 1995

Five specimens of a pronocephalid digenean were identified as *H. lobatus*. This species was originally described as *Glyphicephalus lobatus* by Looss (1901) but was transferred to *Pleurogonius* Looss, 1901 by Ruiz (1946) and later redescribed by Caballero et al. (1955). In the classification of Pronocephalidae proposed by Pérez-Ponce de León and Brooks (1995a), they mentioned that *Himasomum* Linton, 1910 and *Glyphicephalus lobatus* Looss, 1901 form a distinct group from *Pleurogonius* and *Glyphicephalus*. *Himasomum* was recognized as a valid genus, and Pérez-Ponce de León and Brooks (1995a) proposed that *Glyphicephalus lobatus* be reclassified as *Himasomum lobatus*.

This species has been found in *Chelonia mydas* from Egypt, Brazil, and Panamá (Looss, 1901; Ruiz, 1946; Caballero et al., 1955), *Eretmochelys squamosa* (Agassiz, 1857) from the Philippines (Palao Islands, Looss, 1902), and *E. imbricata*

from the United States (Florida), Jamaica (Yamaguti, 1971) and Puerto Rico (Fischthal and Acholonu, 1976; Dyer et al., 1991).

***Pyelosomum renicapite* Poche, 1926**

Thirty-one specimens, 15 mature and 16 immature, were identified as *P. renicapite*. Genus *Pyelosomum* contains 6 species originally placed by Yamaguti (1971) in 4 genera: *Pyelosomum* Looss, 1899; *Epibathra* Looss, 1902; *Astrorchis* Poche, 1925; and *Myosaccus* Gilbert, 1938. A comparative morphological study by Pérez-Ponce de León and Brooks (1995b) supports the placement of 6 species in the genus *Pyelosomum*, and this idea is in agreement with earlier suggestions by Ruiz (1946).

P. renicapite has been previously described from *Dermochelys coriacea* (Linnaeus, 1766) and *Caretta caretta* collected along the Atlantic coast of North America (Luhman, 1935; Yamaguti, 1971; Threlfall, 1978).

***Pachypsolus irroratus* (Rudolphi, 1819)
Looss, 1902**

Two hundred twenty-five worms were identified as *Pachypsolus irroratus*. Until 1982, 7 species were included in the genus *Pachypsolus* Looss, 1901. Blair and Limpus (1982), studying the variability of the type species *P. irroratus*, subsequently proposed a reclassification in the specific composition of this genus. Their examination of the distribution of vitellaria and number of blind anterior caecal diverticula led them to declare all current species to be synonyms of *P. irroratus*, except *P. sclerops* (Travassos, 1922) Travassos, 1928. *Pachypsolus sclerops* was originally described from crocodilians in South America and the rest of the species had been described from marine turtles.

Following the proposal of Blair and Limpus (1982), the hosts for *P. irroratus* are *Caretta caretta*, *Chelonia mydas*, and *Eretmochelys imbricata*, with a worldwide distribution including the Mediterranean Sea; the Red Sea; the Atlantic coast of northwest Africa; Florida, U.S.A.; Puerto Rico; the Pacific coasts of Panama and México; New Guinea; and Australia (Yamaguti, 1971; Ernst and Ernst, 1977; Blair and Limpus, 1982).

***Enodiotrema megachondrus* (Looss, 1899)
Looss, 1901**

Nine hundred five plagiorchids were identified as *Enodiotrema megachondrus* based on the de-

scription given by Looss (1901) and redescrptions made by Caballero-Rodriguez (1960), Euzet and Combes (1962), and Parra (1983). According to Blair and Limpus (1982), 7 species should be included in this genus: *E. megachondrus* (type species); *E. reductum* Looss, 1901; *E. instar* Looss, 1901 and *E. acariaeum* Looss, 1902 from the intestines of *Caretta caretta* and *Chelonia mydas* in Egypt (Looss, 1901); *E. microvitellatus* Chattopadhyaya, 1972 and *E. schikhobalovae* Gupta and Mehrotra, 1976 from the digestive tract of *Eretmochelys imbricata* in India; and *E. carettae* Blair and Limpus, 1982 from the liver and gall bladder of *Caretta caretta* in Australia. The known geographical distribution of *E. megachondrus* includes Egypt, France (Yamaguti, 1971), Acapulco (Caballero-Rodriguez, 1960), and Manzanillo (Parra, 1983) along the Pacific coast of México.

***Orchidasma amphiorchis* (Braun, 1899)
Braun, 1901**

Seventy-one telorchids were identified as *O. amphiorchis*. This species was originally described as *Distomum amphiorchis* Braun, 1899 from the intestine of *Caretta caretta* in the Adriatic Sea and renamed *Orchidasma amphiorchis* (Braun, 1899) Braun, 1901. Later, 2 more species were described from sea turtles in India: *Orchidasma indica* Simha, Rao, and Chattopadhyaya, 1971 and *Orchidasma vitelloconfluens* Rao, 1972. Both are considered synonyms of *O. amphiorchis* by Blair and Limpus (1982). This telorchid represents a monotypic genus with a worldwide distribution and is found in 5 species of marine turtles (Blair and Limpus, 1982): *Caretta caretta*, *Eretmochelys imbricata*, *Chelonia mydas*, *Lepidochelys olivacea*, and *Podocnemys expansa* Schwergger, 1812. It was previously described in México by Caballero (1962) from Tamaulipas in the Gulf of México (in *Chelonia mydas*) and Salina Cruz, Oaxaca, on the Pacific coast (in *Eretmochelys imbricata*) by Caballero and Zerecero (1950).

***Prosorchis psenopsis* Yamaguti, 1934**

Three adult specimens were identified as *Prosorchis psenopsis*. The genus *Prosorchis* was created by Yamaguti (1934) to include specimens that apparently were hemiurids but unique in the preacetabular position of the testis. Interestingly, these digeneans are typically found in the gut and occasionally in the body cavity of marine teleosts. This is the first record of this worm from

Table 2. Prevalence and abundance of digeneans in 32 Olive Ridley's turtles (*L. olivacea*) from Oaxaca, México.

Digenean	Number infected (%)	Abundance mean \pm SD
<i>Adenogaster serialis</i>	17 (53.1)	9.3 \pm 4.1
<i>Himasomum lobatus</i>	1 (3.12)	0.2 \pm 0.8
<i>Pyelosomum renicapite</i>	5 (15.6)	1.0 \pm 3.4
<i>Pachysolus irroratus</i>	4 (12.5)	7.0 \pm 32.4
<i>Enodiotrema megachondrus</i>	14 (43.7)	28.2 \pm 65.0
<i>Orchidasma amphiorchis</i>	5 (15.6)	7.7 \pm 11.2
<i>Prosorthis psenopsis</i>	2 (6.2)	0.1 \pm 0.4
<i>Calycodes anthos</i>	11 (34.4)	12.8 \pm 14.8

the intestine of a marine turtle. *Prosorthis psenopsis* was described originally by Yamaguti (1934) from the esophagus of *Psenopsis anomala* (Temminck and Schlegel, 1844) in Japan. This phenomenon could represent an accidental infection; however, phylogenetic analysis by Pérez-Ponce de León and Brooks (1995a) suggests evidence for host-switching among members of the Pronocephalidae. These authors found 3 host-shifts from marine turtles to fish within the pronocephalid digeneans, so the reverse event should also be possible.

Calycodes anthos (Braun, 1899) Looss, 1901

One hundred ninety-two specimens were identified as *Calycodes anthos*. Our specimens were identical to those redescribed by Parra (1983) from *Chelonia mydas* in Manzanillo, México. This species was originally described by Braun in a chelonian from Japan (host species and locality unknown) and later from *Thalassochelys mydas* (= *C. mydas*) from Egypt and Panama (Yamaguti, 1971). Fischthal and Acholonu (1976) described a second species in the genus, *C. caborjoensis*, but the description is based solely on the holotype. The establishment of a new species with only one specimen lacks taxonomic weight. Since we could not examine the original material, we consider *C. caborjoensis* as species inquirendae. Thus, *Calycodes* is still a monotypic genus.

Digenean infracommunity structure

Amphibians and reptiles represent excellent systems in which to study ecological and evolutionary relationships determining helminth species distribution and abundance (Aho, 1990). Helminths of marine turtles have been studied since the last century and, to date, many digenetic trematodes of most turtle species through

the world have been determined (Looss, 1901, 1902; Caballero, 1954; Caballero et al., 1955; Chattopadhyaya, 1972; Rao, 1975; Fischthal and Acholonu, 1976; Ernst and Ernst, 1977; Blair and Limpus, 1982; Dyer et al., 1991; this investigation). However, these studies have focused on taxonomic aspects and include little ecological or evolutionary information to be used as a comparative framework.

Twenty-four of the 32 turtles analyzed were parasitized by digenetic trematodes. No other helminths were found in our samples. Although Sey (1977) found *Porrocaecum sulcatum* (Rudolphi, 1819), *Kathlania leptura* (Rudolphi, 1819), and an unidentified larval trypanorhynch in *Caretta caretta*, our examination of *L. olivacea* found no helminths other than digeneans. Whether the 8 species we collected represent the entire community of gastrointestinal helminths of *L. olivacea* or only a subset of the assemblage can only be resolved by further studies. Resolving this question may be difficult because collection of marine turtles is now prohibited in México and in most places throughout the world.

The prevalence and abundance of infection of each digenean species is presented in Table 2. The digenean infracommunity was numerically dominated by *Enodiotrema megachondrus* with abundance of 28.2 ± 65.2 individuals/analyzed host. Three species of flukes, *E. megachondrus*, *Adenogaster serialis*, and *Calycodes anthos*, were relatively common, with prevalences between 34.4% and 53.1%, and accounted for 79% of all individuals (Table 2). Individual turtles harbored between 1 and 5 species. Hosts with more than 2 species were rare (37.5%) with 62.5% of the infected turtles harboring 1 or 2 species of digeneans. The mean species richness was 1.8 ± 1.4 for each analyzed host. The lowest number of worms per infracommunity was 1 and the highest was 365 (average 49.9 ± 88.7). Twenty-

five percent of examined turtles were found free of digeneans. Brillouin's index ranged from 0.37 to 1.6, with a mean value of 0.42 ± 0.47 . Qualitative as well as quantitative faunal similarity for all pairwise comparisons among hosts were quite low, with a mean value of $39.5 \pm 30.8\%$ (Sorensen coefficient) and $17.2 \pm 27.9\%$ (percent similarity) indicating high disparity in the number of individuals and the presence-absence of species across infracommunities.

In the literature, we found previous reports about helminth communities only in freshwater turtles. Some attempts have been made in this group of hosts to correlate the structure of helminth communities with geographic location or habitat conditions (Esch and Gibbons, 1967; Esch et al., 1979a, 1979b) but they do not provide data at the infracommunity level. As far as we know, the only documented study at this level besides the revision by Aho (1990) is Jacobson (1987, cited in Esch et al., 1990) in which the infra- and component community structure of intestinal helminths of the yellow-bellied slider, *Trachemys scripta* Schoepff, 1792 was examined. This author found a similar value for diversity index (0.46) to the value found in our study (0.41).

Our results are quite similar to those shown by Aho (1990) for the Testudines group for the mean species richness per individual host (1.8 ± 1.14 vs. 1.52 ± 0.20) and the mean number of worms (49.9 ± 88.7 vs. 66.6 ± 21.9). It is important to emphasize that the diversity obtained for Olive Ridley's turtle is greater than for most terrestrial and freshwater turtles and yet only digeneans were found in our analysis.

In this work we consider the digenean infracommunity of *L. olivacea* to be depauperate and isolationist in character, in accordance with the features established by Holmes and Price (1986).

The factors we consider to be the most important in determining the diversity, richness, and number of worms of the infracommunities are vagility of the host, feeding habits, and the mixture of turtle populations arriving at the nesting sites. The low similarity patterns between infracommunity pairs may also be the result of a combination of these factors. Additionally, the fact that these turtles remain in warm waters throughout much of their lives increases metabolic rate and input of food, exposing each host to frequent infections with different species of parasites.

Lepidochelys olivacea is the most numerous marine turtle today (Zwinnenberg, 1976) and is

widely distributed. It occurs in the east and west Pacific Ocean, in the Indian Ocean, and in both sides of the Atlantic Ocean (Bowen et al., 1991). The long distance movements of turtle populations between nesting and feeding sites increase the exposure to a variety of helminth species and contribute to the development of more complex helminth communities (see Kennedy et al., 1986). However, the high vagility and mixing of populations in breeding areas may limit the development of helminth infracommunities that are qualitatively and quantitatively predictable among individuals. These aspects need to be determined in further studies.

There is no available information on the life cycle patterns of the digeneans found, but the turtles may have become infected by the ingestion of different kinds of food. Olive Ridley's turtle is omnivorous and feeds on different marine invertebrates such as crabs, shrimp, molluscs, bryozoans, sipunculids, and ascidians, as well as fish eggs. It also feeds on fish and vegetation (Montenegro et al., 1986). The presence of pronoccephalids demonstrates that vegetation could be an important part of the diet of this host.

Additionally, information about the host-specificity of the digeneans mentioned herein shows that all of them can be considered as host generalists; although they all are parasites of marine turtles (with the exception of *P. psenopsis*), each has been recorded in 3 or 4 different host species.

The main goal of this paper was to provide information about the digenean infracommunity structure of *L. olivacea* as well as data to be used in the future to answer some of the questions addressed by Aho (1990, p. 162). We believe that our results force us to consider a different approach to analysis of the factors that determine the helminth community structure in reptiles. Many factors have been proposed as determinants of helminth community structure in different kinds of hosts, such as the habitat of the host (aquatic, semiaquatic, terrestrial), host feeding type (herbivorous, omnivorous, carnivorous), host vagility, etc. Most comparisons use nonphylogenetic classifications of vertebrates and, as a result, it has been proposed that the helminth richness and abundance increases according with the place of hosts within this classification (Freshwater Fish-Amphibians and Reptiles-Birds-Mammals) (see Bush et al., 1990). We propose to address questions concerning the

ecological determinants of helminth community structure between closely related groups of hosts, i.e., the chelonians should be compared with their sister group, the Sauria, and the paraphyletic reptiles should be compared with birds within the monophyletic amniota, and comparisons between reptiles and amphibians just because they are ectotherms, or between birds and mammals as endotherms, should be avoided.

There is still need for more information from many different reptile-parasite systems in order to be able to produce testable hypotheses to explain the causes of observed helminth community patterns. In summary, we must keep collecting more data about helminth communities of marine turtles and integrating this information, using a well-developed and robust method like that proposed by Brooks and McLennan (1991, 1993). We may then be able to decipher the complex evolutionary and biogeographical history of helminth-marine turtle associations and have clues to a better understanding of parasite community evolution.

Acknowledgments

We thank Mónica Harada, Rocío Hernández, David Osorio, and Berenit Mendoza for their cooperation in the field work, and Mónica Harada for stain and mount specimens. We are grateful to Scott Monks, University of Toronto, for critical review of the manuscript and to two anonymous reviewers who made invaluable suggestions for the improvement of the manuscript. This research was funded by the Consejo Nacional de Ciencia y Tecnología (CONACyT) No. P020CCOR892283. Publication was supported by the Brayton H. Ransom Memorial Trust Fund.

Literature Cited

- Anonymous.** 1988. Mexico's sea turtle program. *Marine Fisheries Review* 50:70-72.
- Aho, J. M.** 1990. Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. Pages 157-195 in G. W. Esch, A. O. Bush, and J. M. Aho, eds. *Parasite Communities: Patterns and Processes*. Chapman and Hall Publishers, London.
- Blair, D., and C. J. Limpus.** 1982. Some digeneans (Platyhelminthes) parasitic in the loggerhead turtle, *Caretta caretta* (L.), in Australia. *Australian Journal of Zoology* 30:653-680.
- Bowen, W. B., A. B. Meylan, and J. C. Avise.** 1991. Evolutionary distinctiveness of the endangered Kemp's Ridley sea turtle. *Nature* 352:709-711.
- Brooks, D. R., and D. A. McLennan.** 1991. Phylogeny, Ecology and Behaviour: A Research Program in Comparative Biology. University of Chicago Press, Chicago. 434 pp.
- , and ———. 1993. *Parascript: Parasites and the Language of Evolution*. Smithsonian Institution Press, Washington. 429 pp.
- Bush, A. O., J. M. Aho, and C. R. Kennedy.** 1990. Ecological versus phylogenetic determinants of helminth parasite community richness. *Evolutionary Ecology* 4:1-20.
- Caballero y C., E.** 1954. Helminths of the República de Panamá. X. Algunos Tremátodos de *Chelone mydas* (L.) tortuga marina comestible del Océano Pacífico del Norte. *Anales de la Escuela Nacional de Ciencias Biológicas I.P.N.* 8:31-58.
- . 1962. Tremátodos de las Tortugas de México. X. Presencia de *Orchidasma amphiorchis* (Braun, 1899) Looss, 1900 en una tortuga marina, *Chelonia mydas* de las costas del Estado de Tamaulipas, México. *Anales Instituto Biología Universidad Nacional Autónoma de México* 33: 47-55.
- , and M. C. Zerecero. 1950. Tremátodos de las tortugas de México. VI. Revista Médica Veterinaria de Parasitología (Caracas) 9:123-132.
- , and R. G. Grocott. 1955. Helminths of the República de Panamá. XV. Tremátodos de *Chelone mydas* (L.) tortuga marina comestible del Océano Pacífico del Norte. 2a parte. *Anales Instituto de Biología UNAM, México* 26:149-191.
- Caballero-Rodríguez, G.** 1960. Estudio de tremátodos digéneos de algunas tortugas comestibles de México. Tesis Profesional, Facultad de Ciencias, Universidad Nacional Autónoma de México. 69 pp.
- Casas A., G.** 1978. Análisis de la anidación de las tortugas marinas del género *Lepidochelys* en México. *Anales del Instituto de Ciencias del Mar y Limnología Universidad Nacional Autónoma de México* 5:141-158.
- Chattopadhyaya, D. R.** 1972. Studies on the trematode parasites of reptiles found in India. Contribution to our knowledge of the family Pronocephalidae Looss, 1902. *Rivista di Parassitologia* 33: 99-124.
- Dyer, W. G., E. H. Williams, and L. Bunkley-Williams.** 1991. Some digeneans (Trematoda) of the Green Turtle, *Chelonia mydas* (Testudines: Cheloniidae) from Puerto Rico. *Journal of the Helminthological Society of Washington* 58:176-180.
- Enciso, S. G., and J. Barajas.** 1993. Evaluación de la importancia de la playa de anidación Morro Ayuta, Oaxaca para la reproducción de la tortuga golfina *Lepidochelys olivacea* (Eschscholtz) y estudio de algunos aspectos de su biología durante la temporada de anidación de 1988. Tesis Profesional, Facultad de Ciencias, Universidad Nacional Autónoma de México, México. 110 pp.
- Ernst, E. M., and C. H. Ernst.** 1977. Synopsis of helminths endoparasitic in native turtles of the United States. *Bulletin of the Maryland Herpetological Society* 13:1-75.
- Esch, G. W., and J. W. Gibbons.** 1967. Seasonal incidence of parasitism in the painted turtle, *Chrysemis picta marginatta* Agassiz. *Journal of Parasitology* 53:818-821.

- , J. W. Gibbons, and J. E. Bourque. 1979a. The distribution and abundance of enteric helminths in *Chrysemys scripta* from various habitats on the Savannah River Plant in South Carolina. *Journal of Parasitology* 65:624–632.
- , ———, and ———. 1979b. Species diversity of helminth parasites in *Chrysemys scripta* from a variety of habitats in South Carolina. *Journal of Parasitology* 65:633–638.
- , A. W. Shostak, D. J. Marcogliese, and T. M. Goater. 1990. Patterns and processes in helminth parasite communities: an overview. Pages 1–19 in G. W. Esch, A. O. Bush, and J. M. Aho, eds. *Parasite Communities: Patterns and Processes*. Chapman and Hall, London. 335 pp.
- Euzet, L., and C. Combes. 1962. Deux trématodes digènes de *Thalassochelys caretta* (L.). *Bulletin de la société Zoologique Française* 87:15–22.
- Fischthal, J. H., and A. D. Acholonu. 1976. Some digenetic trematodes from the Atlantic hawksbill turtle, *Eretmochelys imbricata imbricata* (L.), from Puerto Rico. *Proceedings of the Helminthological Society of Washington* 43:174–185.
- Frazier, J. G. 1983. Análisis estadístico de la tortuga golfinia *Lepidochelys olivacea* (Eschscholtz) de Oaxaca, México. *Ciencia Pesquera* 4:49–75.
- Groschafft, J. A., and F. Tenora. 1981. Recognition of suborder Notocotylata (Trematoda). *Acta Scientiarum Academiae Scientiarum Bohemoslovaca*, Brno 15:1–46.
- Holmes J. C., and P. W. Price. 1986. Communities of Parasites. Pages 187–213 in J. Kikkawa and D. J. Anderson, eds. *Community Ecology: Patterns and Process*. Blackwell Scientific Publications, Melbourne.
- Kennedy, C. R., A. O. Bush, and J. M. Aho. 1986. Patterns in helminth communities: why are birds and fish different? *Parasitology* 93:205–215.
- Looss, A. 1901. Ueber Trematoden aus Seeschildkroten der ägyptischen Küsten (Notizen zur Helmentologie Egyptens. IV.) *Zentralblatt für Bakteriologie, Parasitenkunde und Infektionskrankheiten, Erste Abteilung Originale* 30:555–569, 618–625.
- . 1902. Ueber neue und bekannte Trematoden aus Seeschildkröten. Nebst Erörterungen zur Systematik und Nomenclatur. *Zoologische Jahrbücher, Abteilung für Systematik, Oekologie und Geographie der Tiere* 16:411–894.
- Luhman, M. 1935. Two new trematodes from the loggerhead turtle (*Caretta caretta*). *Journal of Parasitology* 21:274–276.
- Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *Journal of Parasitology* 68:131–133.
- Márquez, M. R., A. Villanueva, and C. Peñaflores. 1976. Sinopsis de datos biológicos sobre la tortuga golfinia *Lepidochelys olivacea* (Eschscholtz, 1829). Instituto Nacional de la Pesca No. 2. 61 pp.
- Montenegro S. B., N. G. Bernal, and A. Martinez. 1986. Estudio del contenido estomacal de la tortuga marina *Lepidochelys olivacea* en la costa de Oaxaca, México. *Anales del Instituto de Ciencias del Mar y Limnología. Universidad Nacional Autónoma de México* 13:121–132.
- Parra R., L. 1983. Estudio de Algunos Monogéneos y Tremátodos Parásitos de Reptiles de México. Tesis Profesional, Facultad de Ciencias, Universidad Nacional Autónoma de México. 117 pp.
- Peñaflores, S. C., and E. J. Nataren. 1988. Resultados de acciones protectoras para las tortugas marinas en el Estado de Oaxaca. *Los Recursos Pesqueros de México*. 350 pp.
- Pérez-Ponce de León, G., and D. R. Brooks. 1995a. Phylogenetic relationships of the genera of the Pronocephalidae Looss, 1902 (Digenea: Paramphistomiformes). *Journal of Parasitology* 81:267–277.
- , and ———. 1995b. Phylogenetic relationships among the species of *Pyelosomum* Looss, 1899 (Digenea: Pronocephalidae). *Journal of Parasitology* 81:278–280.
- Perez-Vigueras, I. 1955. Contribución al conocimiento de la fauna helmintológica cubana. *Memorias de la Sociedad Cubana de Historia Natural* 22:21–71.
- Pielou, E. C. 1975. *Ecological Diversity*. Wiley-Interscience, New York. 165 pp.
- Rao, L. S. 1975. Studies on the trematode parasites of turtles from India. Further contribution to our knowledge of the family Pronocephalidae Looss, 1902. *Rivista di Parassitologia* 36:137–151.
- Ruiz, J. M. 1946. Pronocephalidae (Trematoda). *Estudos das Espécies Brasileiras e Revisao da Familia*. *Memorias Instituto Butantan* 19:249–372.
- Sey, O. 1977. Examination of helminth parasites of marine turtles caught along the Egyptian coast. *Acta Zoologica Academiae Scientiarum Hungaricae* 23:387–394.
- Threlfall, W. 1978. Three species of Digenea from the Atlantic leatherback turtle (*Dermochelys coriacea*). *Canadian Journal of Zoology* 57:1825–1829.
- Waldichuk, M. 1987. Sea turtles—endangered species. *Marine Pollution Bulletin* 18:623–627.
- Yamaguti, S. 1934. Trematodes of fishes. *Japanese Journal of Zoology* 5:249–541.
- . 1971. *Synopsis of Digenetic Trematodes of Vertebrates*. Vol. I, II. Keigaku Publishing Co., Tokyo, Japan. 1,074 pp.
- Zwinnenberg, A. J. 1976. The Olive Ridley, *Lepidochelys olivacea* (Eschscholtz, 1829): probably the most numerous turtle today. *Bulletin of the Maryland Herpetological Society* 13:75–95.